Phylogenetic Tests of Evolutionary Scenarios: the Evolution of Flightlessness and Wing Polymorphism in Insects

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ABSTRACT

Secondary loss of the flight ability has occurred in nearly all winged orders of insects, many times within most orders, and probably hundreds of times within the Hemiptera and Coleoptera. Loss of flight may be an attribute of all individuals of a species, of only one sex (usually the female), or populations may be polymorphic, composed of both flying and flightless individuals, eventually with a seasonal variation in frequencies. Since flightlessness is linked to a multitude of morphological, physiological, and ecological components that are of great evolutionary significance, flight loss and wing polymorphism in insects have received much attention in recent years. The present paper focus on the role phylogenetic inference can play in clarifying evolutionary patterns of flightlessness in insects and possible causes of the loss of flight ability. This approach is here exemplified using the orders of pterygote insects, the families of Hemiptera-Heteroptera (true bugs), the genera of the heteropteran family Gerridae (water striders), and the species of the water strider genera *Limnoporus*, *Aquarius*, and *Gerris*. Cladograms can be used to track associations between flightlessness and other factors as well as the relative evolutionary success of flying and flightless sister groups. However, phylogenetic inference applied to higher taxonomic levels presents many problems as exemplified by the orders of pterygote insects and the families of Hemiptera-Heteroptera. In many cases obligatory loss of wings coincides with a significant change in way of life, *e.g.*, ectoparasitism or marine habit, but it is rarely possible to tell which came first. It is argued that phylogenetic inference are most effectively applied at lower taxonomic levels, in particular to monophyletic groups of species with varying expressions of wing polymorphism. In species of northern temperate water striders (Heteroptera, Gerridae), phylogenetic inference shows definite associations between flight loss and durational stability of habitats. Contrary to previous hypotheses, the winged state is not the ancestral one. Surprisingly, the ancestors are inferred to be predominantly flightless or permanently dimorphic, occupying relatively stable habitats. Subsequent evolution of long-wingedness or seasonal dimorphism has allowed descendant taxa to colonize less stable habitats.

RÉSUMÉ

Tests phylogénétiques de scénarios évolutifs : l'évolution de la perte du vol et du polymorphisme alaire chez les Insectes

La perte secondaire de la capacité à voler a eu lieu dans presque tous les ordres ailés d'insectes, de nombreuses fois chez la plupart des ordres, et probablement des centaines de fois chez les Hémiptères et les Coléoptères. La perte du vol peut être un attribut de tous les individus d'une espèce, ou de l'un des sexes (le plus souvent les femelles), ou bien encore les populations peuvent être polymorphes, c'est à dire composées d'individus capables ou incapables de voler, avec la possibilité d'une variation saisonnière de leur fréquence. La perte du vol et le polymorphisme alaire chez les insectes ont été l'objet de beaucoup d'intérêt ces dernières années, parce qu'ils sont liés à une multitude de composantes morphologiques, physiologiques, et écologiques qui sont d'une grande importance dans le domaine de l'évolution. L'étude présente concerne le

rôle de l'inférence phylogénétique dans la clarification des séquences évolutives de la perte du vol chez les insectes et des causes possibles de cette perte. Cette étude prend en compte les ordres d'insectes Ptérygotes, les familles d'Hémiptères-Hétéroptères (punaises), des genres d'Hétéroptères Gerridae (patineurs), et des espèces des genres de patineurs *Limnoporus*, *Aquarius*, et *Gerris*. Les cladogrammes peuvent être utilisés pour retracer non seulement les associations entre la perte du vol et d'autres facteurs mais aussi le succès évolutif relatif de groupes-frères respectivement capables et incapables de voler. Cependant, l'inférence phylogénétique appliquée aux plus hauts niveaux taxonomiques pose de nombreux problèmes comme c'est le cas des ordres d'insectes Ptérygotes et des familles d'Hémiptères-Hétéroptères. La perte totale des ailes coïncide de nombreuses fois avec un changement important de mode de vie, *e.g.*, l'ectoparasitisme ou le mode de vie marin, mais il est rarement possible de dire quel changement s'est fait en premier. Il est donc proposé que l'inférence phylogénétique soit utilisée de manière plus efficace et plus judicieuse à de plus bas niveaux taxonomiques, en particulier sur des groupes monophylétiques d'espèces montrant des types variés de polymorphisme alaire. Dans les espèces de patineurs des zones tempérées de l'hémisphère Nord (Hétéroptères, Gerridae), l'inférence phylogénétique montre qu'il existe une nette association entre « perte du vol » et « stabilité continue des habitats dans le temps ». L'état ailé n'est pas ancestral, ce qui est en contradiction avec les hypothèses antérieures. De manière inattendue, les ancêtres sont inférés avoir été en majorité incapables de voler ou constamment dimorphiques, et avoir occupé des habitats relativement stables. L'évolution subséquente vers la possession d'ailes longues et fonctionnelles ou vers un dimorphisme saisonnier a permis aux taxa descendants de coloniser des habitats moins stables.

INTRODUCTION

Flight capability is without doubt one of the primary innovations governing the evolutionary success of insects. However, secondary loss of this capability has occurred in nearly all winged orders of insects, many times within most orders, and probably hundreds of times within the large orders of Hemiptera and Coleoptera. The loss of flight may involve all kinds of modifications of wings and flight musculature. Loss of flight may be an attribute of all individuals of a species, of only one sex (usually the female), or populations may be polymorphic, composed of both flying and flightless individuals and, eventually, with a seasonal variation in frequencies. The largest variability in wing development is observed among water striders (Heteroptera, Gerridae) as illustrated in Fig. 1.

Flightlessness in insects is linked to a multitude of morphological, physiological, and ecological components that are of great evolutionary significance (*e.g.*, HARRISON, 1980; ROFF, 1986, 1990; WAGNER & LIEBHERR, 1992; SPENCE & ANDERSEN, 1994). The production and maintenance of the flight apparatus (wings, flight musculature, etc.) is energetically expensive and bound to compete with other, physiologically equally demanding processes such as the production of oocytes ("oogenesis-flight" syndrome; JOHNSON, 1969). Therefore, one possible advantage of wing loss is that it allows a female insect to divert energy normally used in wing and wing muscle development to the production of more eggs. This could increase the female's fitness more than the advantages associated with the ability to fly (ROFF, 1986, 1990; ROFF & FAIRBAIRN, 1991).

The most widely accepted explanation for loss of the flight ability in insects relates to environmental heterogeneity. SOUTHWOOD (1962: 172) predicted "that within a taxon one should find a higher level of migratory movement in those species associated with temporary habitats than in those species associated with more permanent ones". In his review of the evolution of flightlessness in insects, ROFF (1990) assembled considerable evidence indicating that flightlessness is strongly associated with habitat stability in all major groups of insects. Habitats in which insects have a higher frequency of flightless forms than the average are: woodlands, deserts, mountains, caves, ocean surfaces, termite and hymenopteran nests, and the body surfaces of homeothermic vertebrates (ectoparasites). Flightlessness has also been related to habitat
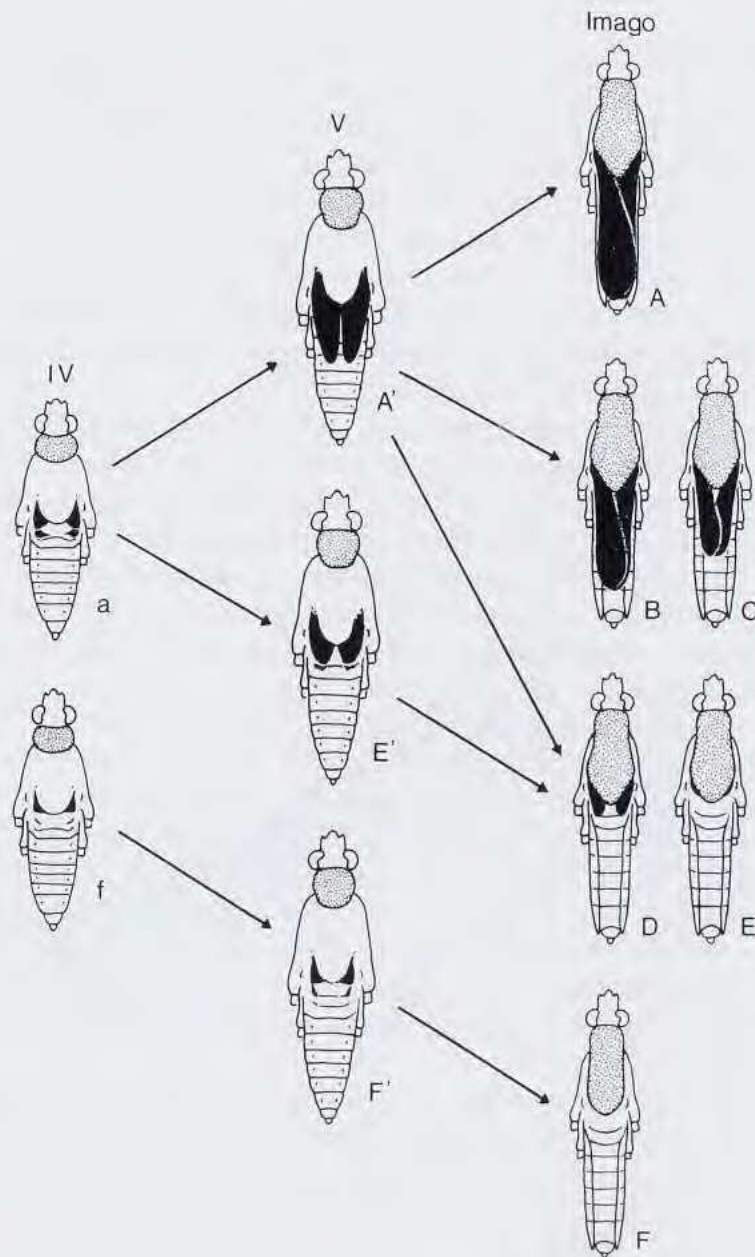
FIG. 1. — Wing polymorphism in water striders (Heteroptera, Gerridae) and different ontogenetical pathways of wing development through fourth (IV) and fifth (V) instar nymphs, and imago. Nymphs and imagines shown without antennae and legs, not drawn to same scale. Further discussion in text. (Reproduced with modification from ANDERSEN, 1982).

isolation. DARWIN's (1872) hypothesis that on oceanic islands a flightless morph would be more fit than a winged morph because it would be less likely to be accidentally blown or fly from the island was, however, questioned by ROFF (1990) who concluded that the proportion of flightless insects on islands was no higher than in continental areas.

Phylogenetic inference

The convergent evolution of flightless adult forms in taxonomically widely separate, primarily winged insect taxa suggests that the loss of flight ability and maintenance of wing polymorphism is a consequence of adaptation through natural selection as first proposed by DARWIN (1872). Nevertheless, previous discussions of the evolution of flightlessness in insects(*e.g.* HARRISON, 1980; ROFF, 1986, 1990; ROFF & FAIRBAIRN, 1991) have largely ignored the historical perspective in explaining patterns of flightlessness in insects. The importance of phylogeny in comparative biological studies is now widely recognized (BROOKS & McLENNAN, 1991; HARVEY & PAGEL, 1991; EGGLETON & VANE-WRIGHT, 1994; GRANDCOLAS *et al.*, 1994; MILLER & WENZEL, 1995) and this approach has recently been applied in studies of the evolution of flightlessness in insects (ANDERSEN, 1993a; ROFF, 1994).

What role can phylogenetic inference play in understanding the evolution of flightlessness in insects? First, reconstructed phylogenies (cladograms) can be used to track the evolutionary fate (*e.g.*, relative rates of speciation and extinction) of flightless and winged sister groups (ROFF, 1994). Second, cladograms may provide the basis for making phylogenetically more relevant comparisons among monophyletic groups (clades). Previously, correlation tests involving flight loss have assumed that every species of a clade represents an independent datum. However, species sharing a trait (*e.g.*, wing loss) inherited from their most recent, common ancestor, do not yield statistically independent data. Cladograms may also be used to predict which species require further study in order to resolve a particular problem. Third and finally, by mapping different states of wing development upon a cladogram, ancestral states can be reconstructed, number of evolutionary transitions between states can be traced, and possible sequences of change can be inferred (ANDERSEN, 1993a). If two attributes are considered at the same time (*e.g.*, wing morphism and type of habitat), the relative position of state changes for the two attributes may be located. If the flight ability was lost *after* a significant change in habitat, flightlessness may be an adaptation to the new habitat. If flight loss preceded the change in habitat, flightlessness may be a prerequisite (exaptation) for the colonization of a new habitat. It is important to remember, however, that in both cases flightlessness may be caused by other, presently unknown factors.

Before using phylogenetic inference in comparative biological studies, the choice of taxonomic level should be seriously considered. Ideally, the attribute(s) in question should vary much between, but only little within the groups selected as terminal taxa. Within-taxon variability presents a major problem in most studies involving higher taxa (families, orders) which are more likely to show within-taxon variation than, *e.g.*, genera and species groups. As a rule, the only solution to the problem of high within-taxon variability is to repeat the analysis with a more finely resolved phylogeny.

MATERIAL AND METHODS

Phylogenies

The phylogenetic relationships between the orders of winged insects (Insecta-Pterygota; Fig. 2) are chiefly based upon KRISTENSEN (1991/1994, 1995) with the following modifications: (1) Plecoptera (stoneflies) are placed as sister group to the remaining Neopteran order (as suggested by KRISTENSEN 1991/1994, p. 132, but not depicted in his cladogram, his Fig. 5.5); (2) Hemiptera and Thysanoptera are treated as genuine sister groups (Superorder Condylognatha) following a more widely accepted hypothesis than joining the thysanopterans with psocodeans (Psocoptera + Phthiraptera); (3) Strepsiptera is placed as sister group of Coleoptera following KUKALOVA-PECK & LAWRENCE (1993). The alleged sister group relationship between Strepsiptera and Diptera (WHITING & WHEELER, 1994) has been seriously questioned by KRISTENSEN (1995).

The primary source for the phylogeny of the Hemiptera-Heteroptera (Fig. 3) is the excellent monograph by Schuh & Slater (1995) supplemented by Andersen (1982, 1995a), Schuh (1986), Schuh & Stys (1991), Wheeler *et al.* (1993), and Mahner (1993). The currently accepted classification of the Heteroptera excludes the southern temperate family Peloriidae (Coleorrhyncha) from the suborder and divides it into seven infraorders (listed by the same order of families as in Fig. 3): Enicocephalomorpha (Aenictopecheidae, Enicocephalidae), Dipsocoromorpha (Ceratocombidae to Stemmocryptidae), Gerromorpha (Mesoveliidae to Gerridae), Nepomorpha (Nepidae to Helotrephidae), Leptopodomorpha (Aepophilidae to Leptopodidae), Cimocomorpha (Pachynomidae to Polyctenidae), and Pentatomomorpha (Aradidae to Rhopalidae). The relationships between these infraorders depicted in the cladogram (Fig. 3) follows Wheeler *et al.* (1993) and Schuh & Slater (1995).
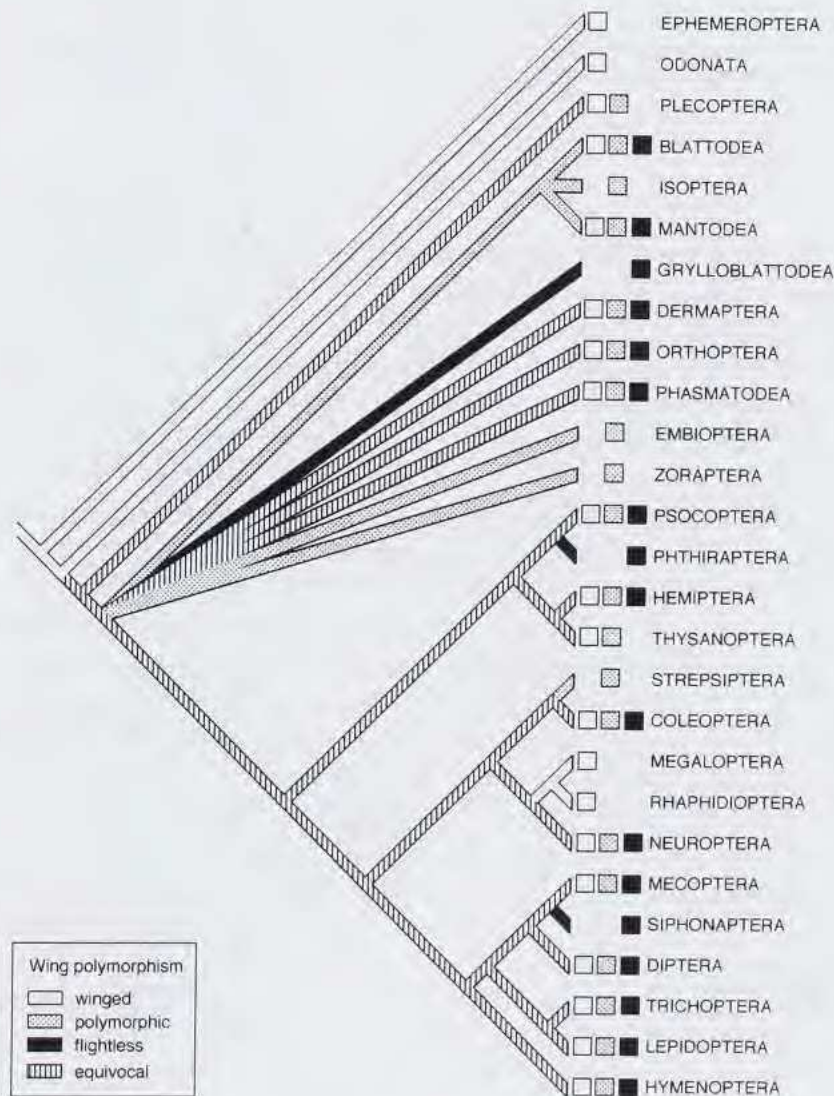

Fig. 2. — Phylogeny and distribution of three states of wing development in the orders of pterygote insects. Further discussion in text.

The phylogenetic relationships between the genera of the family Gerridae (Fig. 4) are primarily based upon MATSUDA (1960) and ANDERSEN (1982, 1995b; and unpublished). Finally, phylogenies for species or species groups of the genera *Aquarius*, *Gerris*, and *Limnoporus* (Fig. 5) are compiled from ANDERSEN (1990, 1993b) and ANDERSEN & SPENCE (1992) with modifications for the last mentioned genus as discussed by SPERLING *et al.* (in press).
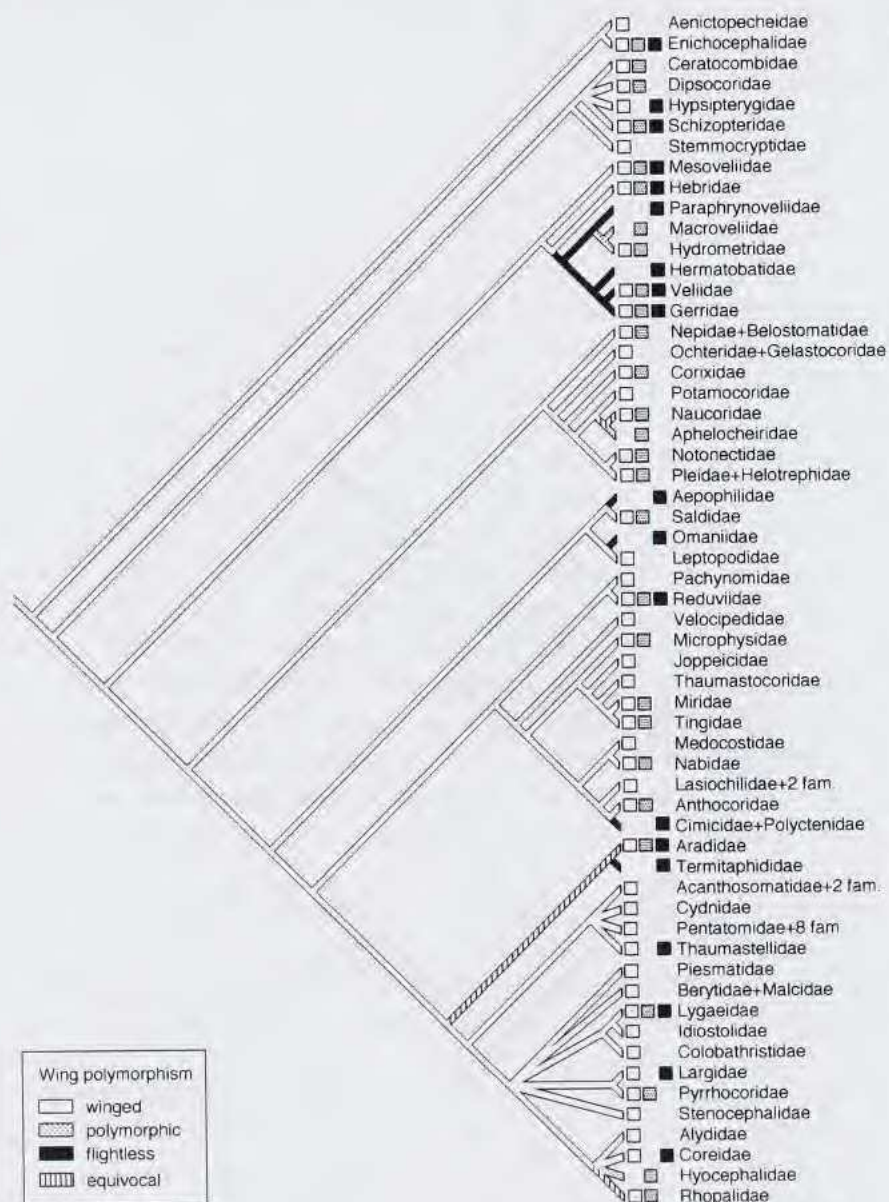

FIG. 3. — Phylogeny and distribution of three states of wing development in the families of Hemiptera-Heteroptera. Further discussion in text.

Wing morph frequencies

A complex terminology (*e.g.*, ANDERSEN, 1982; SCHUH & SLATER, 1995) has been employed to distinguish various degrees of wing modification in flightless and polymorphic insects (apterous, brachypterous, etc.). For the sake of simplicity, I here distinguish between three states of wing morphism in adult insect orders, Heteroptera, and the Gerridae (slightly different states are used for *Aquarius*, *Gerris*, and *Limnoporus*; see below): (1) *winged*; all individuals of a species possess fully developed and presumably functional wings; (2) *polymorphic*; natural populations composed of both winged and flightless adult individuals, the latter sometimes restricted to only one sex; and (3) *flightless*; all individuals of a species flightless. Information on the distribution and frequencies of different wing morphs are chiefly compiled from the following sources: ROFF (1990) and CSIRO & NAUMANN (1991) for the orders of insects; SCHUH & SLATER (1995) for the Hemiptera-Heteroptera; and ANDERSEN (1982, 1990, 1993a, 1993b; ANDERSEN & SPENCE, 1992) for the Gerridae.

Optimization

The evolutionary changes between different states of wing development (treated as non-additive or unordered) were optimized on the cladograms using the computer program MacClade, version 3.05 (MADDISON & MADDISON, 1992) with the "show all most parsimonious states at each node" option. The results of this optimization are shown as different shading of the branches of the cladogram. The shading for "equivocal" is used when the optimization is unable to resolve the state of wing development on a particular branch.

RESULTS AND DISCUSSION

The orders of pterygote insects

In only 4 out of 27 orders of pterygote insects are the adult stage always winged. These are the Ephemeroptera (mayflies) and Odonata (dragonflies, damselflies), previously united in the Palaeoptera, and the small endopterygote orders Megaloptera (alderflies, dobsonflies) and Rhaphidioptera (snakeflies, camelneckflies). Except for the last mentioned order, the immature stage is aquatic in these groups. Flightless adult forms are rare in the Plecoptera (stoneflies), Neuroptera (lacewings), Mecoptera (scorpionflies), and Trichoptera (caddisflies) the first and last order with aquatic immature stages. Relative to the total number of species, flightless or wing polymorphic species are also rare in the large orders Diptera, Lepidoptera, and Hymenoptera.

Obligatorily flightless orders are the Phthiraptera (sucking and chewing lice, Anoplura and Mallophaga) and Siphonaptera (fleas), both ectoparasites on warm-blooded vertebrates, and the small northern temperate order Grylloblattodea.

In the remaining orders, flightlessness or wing polymorphism (sex-bound or not) is common or very common in the exopterygote orders Blattodea (cockroaches), Isoptera (termites, but limited to the worker caste), Mantodea (praying mantids), Orthoptera (grasshoppers, locusts, crickets), Dermaptera (earwigs), Phasmatodea (stick insects), Embioptera (web-spinners), Zoraptera, Hemiptera, and Thysanoptera (thrips). Relative to the total number of species, loss of the flight ability is uncommon in the Coleoptera, but because wing reduction rarely affects the elytra, the flightless adult form is difficult to recognize and its frequency may therefore be underestimated in beetles.

Because of the extremely diverse nature of wing development in most insect orders, the results of the optimization of the three states on the phylogeny of pterygote insects are ambiguous (Fig. 2). Because both palaeopteran orders are obligatorily winged, this undoubtedly was the ancestral state for the Pterygota. The ancestral state for the neopteran orders is equivocal (winged or polymorphic). However, this ambiguity disappears if the Strepsiptera is treated as a subordinate group of Coleoptera (following CROWSON, 1955, and later writings); the winged state is then selected as the ancestral one. The Dictyoptera *s.l.* (Blattodea + Isoptera + Mantodea) were probably primitively wing polymorphic and the Paraneoptera (Psocodea + Hemiptera + Thysanoptera) likewise. It is very unlikely that the ancestors of these groups were

obligatorily flightless since this requires that wings have evolved as (autapomorphic) character reversals in some lineages. Finally, although the ancestral state for the Endopterygota is equivocal, it is predicted that analyses with more finely resolved phylogenies will show, that ancestral endopterygotes were winged like the ancestors of all endopterygote orders except the Strepsiptera and Siphonaptera.
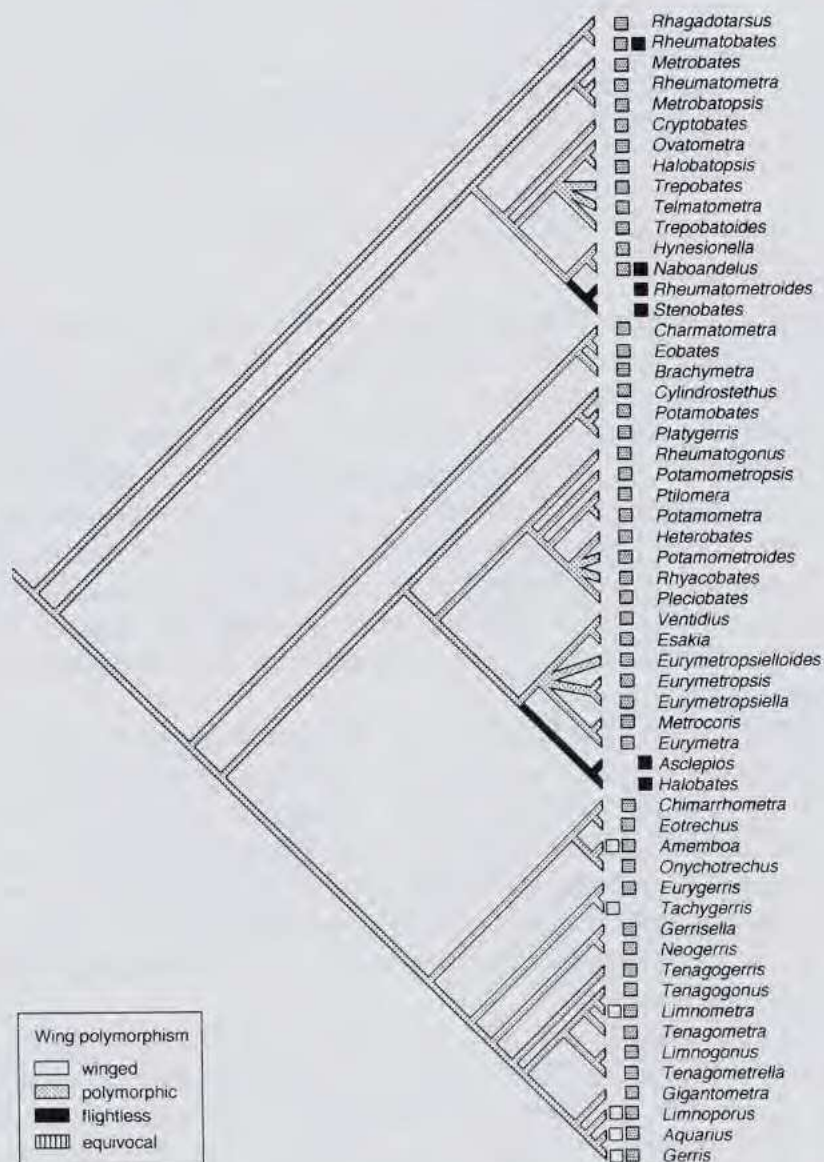

FIG. 4. — Phylogeny and distribution of three states of wing development in the genera of Gerridae (Hemiptera-Heteroptera). Further discussion in text.

At the level of insect orders, phylogenetic inference leading to estimates of the causes underlying patterns of flightlessness is difficult. However, orders with a gradual metamorphosis ("paurometabolous" orders) and with immatures and adults occupying similar niches are more frequently wing polymorphic or flightless than orders with complete metamorphosis and a significant niche shift between the immature and adult stage (ROFF, 1990). To the last category belongs the hemimetabolous orders Ephemeroptera, Odonata, and Plecoptera, and most of the holometabolous orders. Wing polymorphism and flightlessness are also more frequent in orders where adult flight is not an "everyday" activity necessary for feeding, mating, or local dispersal (as the Orthoptera, Hemiptera, and Coleoptera).
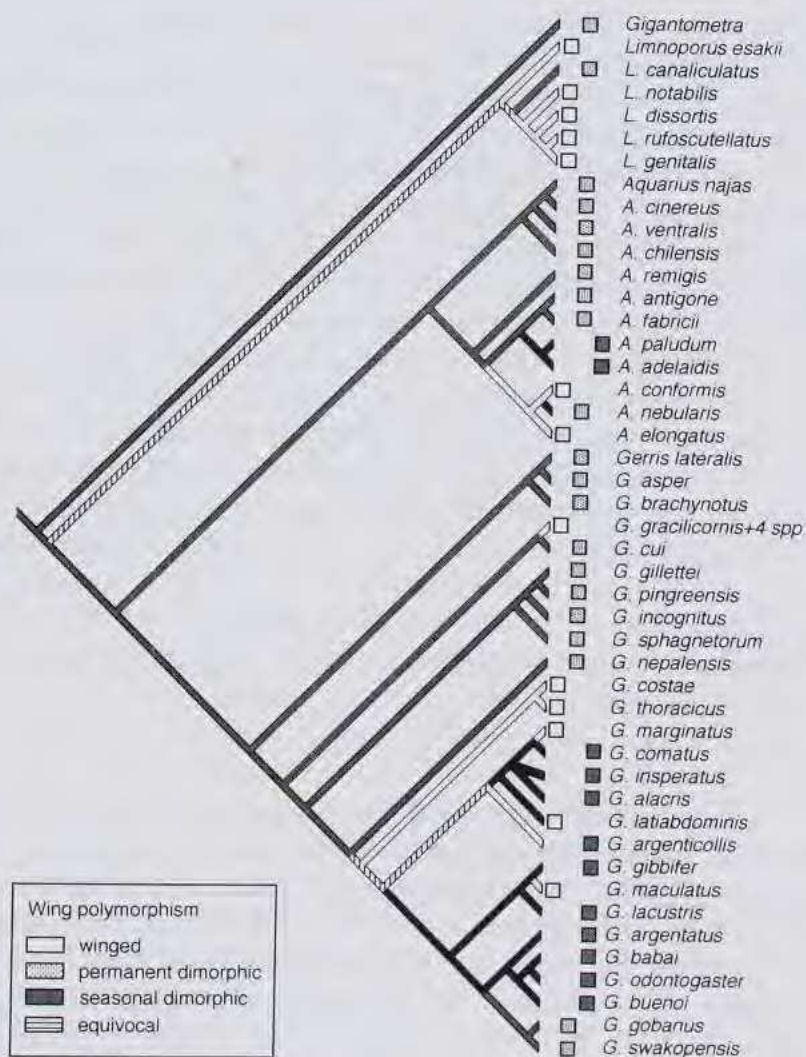

FIG. 5. — Phylogeny and distribution of states of wing development in species belonging to *Aquarius*, *Gerris*, *Gigantometra*, and *Limnoporus* (Hemiptera-Heteroptera, Gerridae). Further discussion in text.

The families of Hemiptera-Heteroptera

The Hemiptera (true bugs, cicadas, plant- and treehoppers, plantlice, etc.) with about 82,000 described species is the largest of the hemimetabolous insect orders. Wing polymorphism is very common and widespread in this order, in particular within the suborder Heteroptera or true bugs where it occurs in 41 out of 75 families (Fig. 3). Flightlessness is especially common in the infraorders Enicocephalomorpha, Dipsocoromorpha, Gerromorpha (semiaquatic bugs), and in the large families Reduviidae (assassin bugs) and Miridae (plant bugs) belonging to the Cimicomorpha, whereas it is relatively rare in the Nepomorpha (aquatic bugs), Leptopodomorpha (shore bugs), and Pentatomomorpha except for the families Aradidae (bark bugs) and Lygaeidae (seed bugs). Obligatorily flightless species are found in the Paraphrynoveliidae, Cimicidae (bed bugs), and Polyctenidae (bat bugs), the last two families being vertebrate ectoparasites, the Termitaphididae (termite inquilines), and in the small marine families Hermatobatidae, Aepophilidae, and Omaniidae.

An optimization of the three states of wing development on the reconstructed phylogeny of the Heteroptera (Fig. 3) unequivocally picks the winged state as the ancestral one for all major lineages. Thus, wing polymorphism and flightlessness have seemingly evolved independently numerous times in true bugs. The flightless state is inferred to be ancestral to the families of Gerromorpha (except Mesoveliidae and Hebridae). The explanation for this result is the presence of two small, obligatorily flightless families (Paraphrynoveliidae and Hermatobatidae) as well as flightless taxa in the large families Veliidae and Gerridae.

At the level of heteropteran families, phylogenetic inference leading to estimates of causality between flightlessness and other attributes is equally problematical. Flightless forms are most frequent in predaceous bugs and in species inhabiting ground litter (Enicocephalidae, most Dipsocoromorpha, the gerromorphan families Mesoveliidae, Hebridae, Paraphrynoveliidae, Macroveliidae, some Leptopodomorpha and Cimicomorpha, and the Lygaeidae), semiaquatic habitats (most Gerromorpha), marine habitats (Hermatobatidae, some Veliidae and Gerridae, Aepophilidae, and Omaniidae), and in ectoparasites (Cimicidae, Polyctenidae, some Lygaeidae), and in those bugs which live under bark (Aradidae and Lyctocoridae). Winged forms are predominant in phytophagous bugs belonging to the family Miridae (Cimicomorpha) and most families of the Pentatomomorpha.

The genera of Gerridae

The Gerridae (water striders) is one of the largest families of semiaquatic bugs (Heteroptera, infraorder Gerromorpha), with about 600 described species. The vast majority of species belonging to this group are wing polymorphic (Fig. 4). Only the genera *Amemboa* (Eotrechinae), *Tachygerris*, *Limnometra*, *Limnoporus*, *Aquarius*, and *Gerris* (Gerrinae) include species which are monomorphic winged. Obligatorily flightless species are restricted to the genera *Rheumatometra* (Rhagadotarsinae), *Naboandelus*, *Rheumatometroides*, *Stenobates* (Trepobatinae), *Asclepios*, and *Halobates* (Halobatinae), all living in marine habitats (from estuaries, mangroves, and intertidal coral reef flats to the open sea).

Ancestral gerrids were probably wing polymorphic (like most gerromorphan bugs; see Fig. 3) and the loss of the flightless form in some species is most likely secondary. Since all marine water striders have polymorphic freshwater relatives, the complete loss of the winged form associated with the extremely stable marine habitats is easily explained. Adult water striders only

use flight for dispersal among habitats and (in temperate regions) in connection with hibernation which takes place on land (ANDERSEN, 1982).

The species of Gerris and related genera

Northern temperate water striders belonging to the genera *Aquarius*, *Gerris*, and *Limnoporus* (formerly united in the genus *Gerris s.l.*) have been extensively used as model organisms in studies of the relations between wing polymorphism, dispersal strategies, and life history dynamics (ANDERSEN, 1973; VEPSÄLÄINEN, 1978; SPENCE, 1989; SPENCE & ANDERSEN, 1994). The phylogeny of the three genera is relatively well understood (ANDERSEN, 1990, 1993b; ANDERSEN & SPENCE, 1992). The cladogram (Fig. 5) shows the relationships between most species belonging to the genera *Limnoporus*, *Aquarius*, *Gerris* with the monotypic genus *Gigantometra* added as outgroup (ANDERSEN, 1995b).

Water striders belonging to this group are either monomorphic winged or wing dimorphic. Following ANDERSEN (1993a), I distinguish between permanent dimorphism in which populations usually include both winged adults (which may be rare) and adults with more or less reduced wings and flight musculature, and seasonal dimorphism in which the flightless adult form only occurs during summer, indicating a direct breeding second generation. The wing development of the two types of flightless forms follow different ontogenetic pathways (Fig. 1). In seasonally dimorphic species, the fourth (IV) and fifth nymphal instar (V) have the same size of wing-pads as nymphs from which the winged adults emerge (a $\rightarrow$ A' $\rightarrow$ A). In permanently dimorphic species, the fourth and fifth instar nymphs have distinctly reduced wing-pads (f $\rightarrow$ F $\rightarrow$ F).

Optimization of the three states of wing development on the cladogram (Fig. 5) points to the permanently dimorphic state as the ancestral one for the whole group as well as for *Aquarius* and *Gerris*, while the wing morphism state is equivocal for the genus *Limnoporus* (one species dimorphic, the rest always winged).

Flightlessness and the "oogenesis-flight" syndrome

The concurrent development in insect ontogeny of the flight apparatus, the ovaries, and the ancillary systems such as the fat-body has been termed the "oogenesis-flight" syndrome (JOHNSON, 1969). The differential development of these systems in response to environmental factors has produced a variety of different forms in insects, ranging from sexually immature, migrant individuals, to various types of flightless, sexually mature, and eventually parthenogenetic or paedogenetic individuals. The wing muscles are relatively massive structures, comprising 10-20 % of the body mass in most insects and undoubtedly consuming a significant proportion of an insect's energy budget (ROFF, 1990). Flightless female insects lack wing muscles and are therefore able to divert more energy to the production of oocytes. In addition, winged females commonly autolyse (self-digest) their flight muscles during egg production as well documented in northern temperate water striders (ANDERSEN, 1973, 1982; FAIRBAIRN & DESRANLEAU, 1987; KAITALA & HULDÉN 1990).

In insects where adult flight is not an "everyday" activity necessary for feeding, mating, and escaping from temporary or deteriorating habitats, it can be predicted that patterns of flightlessness often will be compatible with the "oogenesis-flight" syndrome explanation. The high incidence of flightless forms in the orders Orthoptera, Hemiptera, and Coleoptera, and the

distribution of flightless forms among and within the families of Heteroptera seem to meet this prediction (SCHUH & SLATER, 1995).

Flightlessness and ectoparasitism

Ectoparasites on warm-blooded vertebrates belonging to the orders Phthiraptera, Siphonaptera, Hemiptera-Heteroptera, and Diptera, are all obligatorily flightless. It has been suggested (LYAL, 1985) that the chewing lice (Mallophaga; a paraphyletic group) and sucking lice (Anoplura) evolved from some subgroup of the Psocoptera, namely the family Liposcelidae which contains many flightless species (booklice). If this hypothesis is correct, the phylogeny supports a scenario where loss of flight ability preceded ectoparasitism (Fig. 6). However, the fact that some ectoparasitic Diptera (belonging to the family Hippoboscidae) are winged or dimorphic points at the opposite sequence of evolution, where the parasitic way of life preceded wing loss (WAGNER & LIEBHERR, 1992). In the case of Siphonaptera, its presumed sister group, the Mecoptera, contains both dimorphic and flightless forms. Since ancestral scorpionflies most likely were winged, the loss of flight ability and ectoparasitism in fleas coincide and it is not possible to tell which came first. The situation is the same for the heteropteran families Cimicidae
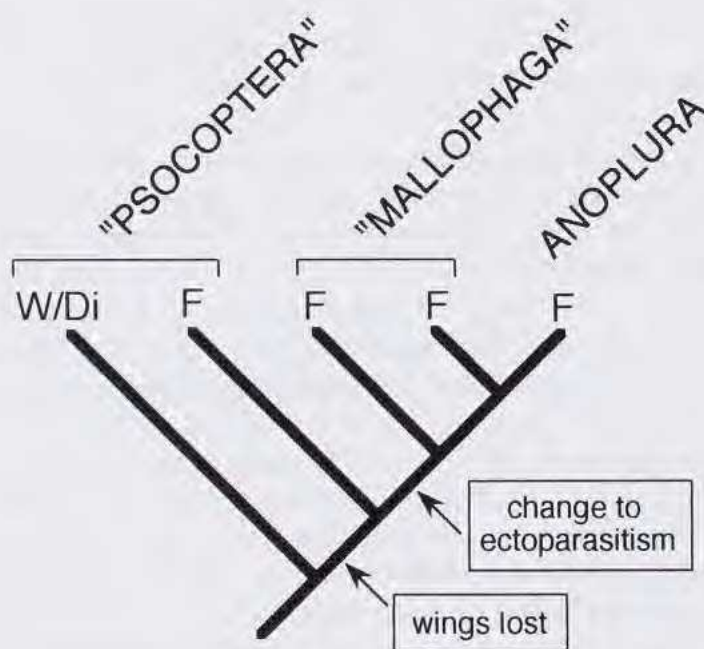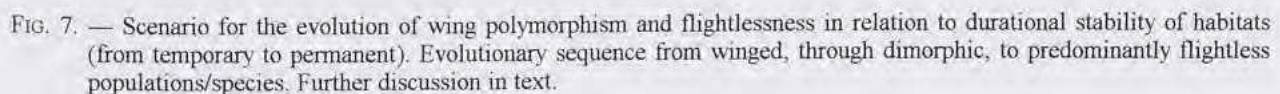

FIG. 6. — Presumed phylogeny and evolution of flightlessness and ectoparasitism in orders of Insecta-Psocodea. Both Psocoptera and Mallophaga are paraphyletic in this phylogenetic hypothesis. Abbreviations: Di, wing dimorphic; F, flightless; W, winged. Further discussion in text.

and Polyctenidae which form a monophyletic group related to the Anthocoridae.

Flightlessness and habitat stability

Phylogenetic tests of scenarios explaining the evolution of flightlessness in relation to habitat are difficult to perform at the level of insect orders as well as the families of Heteroptera. ROFF (1990, 1994) found significant correlation between loss of flight ability with decrease in environmental heterogeneity, with increasing altitude and latitude, but not with isolation (*e.g.*, on oceanic islands). However, the correlation tests performed by ROFF (1990) did not take phylogeny into consideration. In a subsequent paper, ROFF (1994) tried to find methods for correcting his analyses for "phylogenetic effects" using the Orthoptera of North America as example. However, the success of this trial was modest due to a lack of adequate phylogenies for this group of insects.

The currently accepted scenario for the evolution of flightlessness in insects (SOUTHWOOD, 1962; VEPSÄLÄINEN, 1978; HARRISON, 1980; ROFF, 1986) assumes that winged monomorphism

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IN RELATION TO HABITAT**

FIG. 7. — Scenario for the evolution of wing polymorphism and flightlessness in relation to durational stability of habitats (from temporary to permanent). Evolutionary sequence from winged, through dimorphic, to predominantly flightless populations/species. Further discussion in text.

is the original (ancestral) state, and that flightlessness and/or wing polymorphism has evolved through the combined effects of selection against dispersing winged individuals and presumed higher fitness value of non-dispersing, flightless individuals (Fig. 7). In a changing environment where habitats proceed from being relatively unstable (temporary) to increasingly more stable (permanent), populations may change from being monomorphic winged to being wing dimorphic or even purely flightless. If this scenario is applied to a monophyletic group of species which show various degrees of adaptation on a scale of environmental stability, it is predicted that winged species will occupy habitats placed towards the temporary end of the scale while wing dimorphic or flightless species will occupy habitats towards the permanent end of the scale. A hypothetical phylogeny which meets this prediction is shown in Fig. 8.

Although this scenario has intuitive appeal, it should be submitted to phylogenetic tests using real insects before it is used as a general explanatory model for the evolution of flightlessness in relation to habitat. Phylogenetic inference involving temperate water striders of the genera *Aquarius* and *Gerris* (ANDERSEN, 1993a), confirmed that patterns of wing polymorphism were related to habitat stability. However, contrary to the predictions (Fig. 8), the winged state is not the ancestral one. Surprisingly, the ancestors are inferred to be predominantly flightless or permanently dimorphic (Fig. 5), occupying relatively stable habitats. Subsequent evolution of long-wingedness or seasonal dimorphism has allowed descendant taxa to colonize less stable habitats. Thus, patterns of wing polymorphism in temperate water striders are more compatible with the hypothetical phylogeny shown in Fig. 9.

It is relatively straightforward to extend this approach to encompass other biological important traits beside the potential for dispersal, *e.g.*, fecundity, length of reproductive period, pressure from parasitoids and predators, reproductive strategies and mating systems (SPENCE, 1989; ANDERSEN, 1993a, 1994, 1996; SPENCE & ANDERSEN, 1994). Among other things, this approach allows predictions about where mechanisms of determination of adaptive traits may
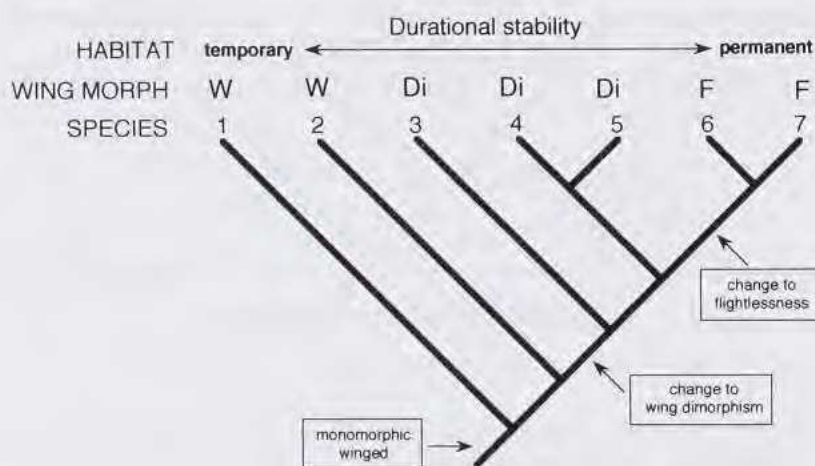

FIG. 8. — Phylogenetical relationships between species 1-7 and patterns of wing morphism compatible with the scenario in Fig. 7. Abbreviations: Di, wing dimorphic; F, flightless; W, winged adult morph. Further discussion in text.
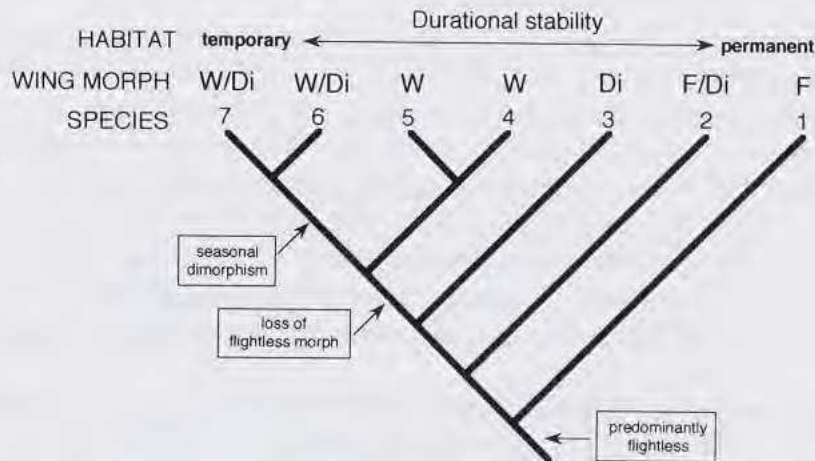
FIG. 9. — Phylogenetical relationships between species 1-7 and patterns of wing morphism compatible with the observed pattern of wing polymorphism in northern temperate water striders belonging to the genera *Aquarius* and *Gerris* (see Fig. 5). Abbreviations as in Fig. 8. Further discussion in text.

differ and thus enable us to select the taxa appropriate for generalizations about selective processes leading to a particular kind of adaptation, like flightlessness and wing polymorphism in insects.

CONCLUSIONS

Wing polymorphism and flightlessness are very widespread among the orders of pterygote insects, in particular those orders where adult flight is not an "everyday" activity necessary for feeding, mating, or local dispersal, as in the Orthoptera, Hemiptera, and Coleoptera. Flightlessness is rare where there is a significant niche shift between the immature and adult individual, as in the Ephemeroptera, Odonata, and Plecoptera, and the holometabolous orders Diptera, Lepidoptera, and Hymenoptera. Because most orders of pterygote insects and many families of Hemiptera-Heteroptera are highly variable with respect to wing morphism, phylogenetic inference is not very helpful in disclosing the causes underlying the observed patterns of flightlessness. In general, however, the patterns are compatible with the "oogenesis-flight" syndrome explanation when viewed in a phylogenetic context.

At the generic level of the water strider family Gerridae, the ancestral mode of adaptation was wing dimorphism, and the few cases of winged monomorphism are estimated to be results of secondary loss of the flightless form. As an extension of permanent dimorphism in freshwater species, marine water striders are obligatorily flightless.

Ectoparasites on warm-blooded vertebrates (Phthiraptera, Siphonaptera, some Hemiptera-Heteroptera and Diptera) are all obligatorily flightless. If the chewing lice (Mallophaga) and sucking lice (Anoplura) evolved from some subgroup of the Psocoptera, the phylogeny supports

a scenario where loss of flight ability preceded ectoparasitism whereas the opposite sequence of evolution may apply to the Diptera-Hippoboscidae.

The currently accepted scenario for the evolution of flightlessness in insects assumes that the winged state is ancestral and that wing polymorphism or flightlessness have evolved through the combined effects of selection against dispersing winged individuals and presumed higher fitness value of non-dispersing, flightless individuals. The present study suggests that this scenario should be submitted to phylogenetic tests using real insects before it is used as a general explanatory model for the evolution of flightlessness in relation to habitat. For example, patterns of wing polymorphism in temperate water striders are more compatible with the reverse scenario, where ancestors are predominantly flightless or permanently dimorphic, occupying relatively stable habitats, and their descendants are long-winged or seasonally dimorphic, colonizing less stable habitats.

Finally, the present study emphasizes the need for taking phylogeny into consideration for further understanding of the evolution of flightlessness in insects. It also illustrates the importance of choosing the right taxonomic level and phylogenetic resolution for analysis. When correctly applied, phylogenetic inference applied to patterns of biologically important attributes can make significant contributions towards understanding the causes underlying these patterns and suggests possibilities for process. In the end, however, understanding process will depend on studying process directly.

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